THE PALAEONTOLOGY AND GEOLOGY OF DUNSINANE SITE, RIVERSLEIGH

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The stratigraphy, fossil assemblages and models of formation and post-depositional history of Dunsinane Site, on the western 'arm' of southern Gag Plateau, are described. The fossil vertebrate fauna most resembles the late Oligocene (System A) fauna of White Hunter Site. Rich, exceptionally preserved invertebrate and plant (twigs, leaves, reproductive organs) assemblages occur in nodules of iron oxide-rich flourapatite and as fragments derived from these nodules and appear to have been preserved by early diagenetic microbially-mediated phosphatisation. The sediment is most likely lacustrine and may directly overlie Precambrian sediments. Erosion of overlying sediments and severe chemical weathering may have led to development of the surface lag of insoluble residue which includes phosphatised bone, nodules and other fossil fragments. Relationships of the fossiliferous nodules to the vertebrate fauna and surrounding sediments are not fully determined.

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Dunsinane Site was discovered in 1990 during exploration of southern Gag Plateau at Riversleigh, NW Queensland (Fig. 1A). In one area the surface was strewn with fragments of fossil bone, fossil wood and nodules of rock that contained leaves, wood, other plant material and invertebrates. Dunsinane Site is the only fossil site at Riversleigh containing plants and one of the few yielding arthropods (Archer et al., 1994). The site was also distinctive in that the fossils were associated with a soft, apparently unconsolidated sediment, rather than embedded in solid limestone. Issues to be resolved regarding this site included the nature and provenance of the fossilised plant and arthropod material, and the relationships of this material to other Riversleigh sediments.

CONCEPTS AND TERMINOLOGY

Palaeontological concepts, biostratigraphy and taxonomic classification follow Archer et al. (1994) and Creaser (1997). The terms 'Dunsinane limestone', 'Dunsinane deposit', 'Dunsinane sediment' and 'Dunsinane calcrete' are used here informally.

STRATIGRAPHY AND GEOLOGY

Representative rock types from Dunsinane Site have been examined by powder X-ray diffraction, SEM and thin-sectioning techniques. A sample of 4 nodules was used for destructive analysis. The area around Dunsinane Site is dominated by 4 main rock types: Precambrian quartzite, ferruginised deposits, overlying Tertiary limestone and the Dunsinane limestone.

PRECAMBRIAN QUARTZITE

The grey Precambrian quartzite is a massive, thick tabular- bedded, crystalline pure quartz sediment. This and a laminated chert constitute the terrain around Gag Plateau and form the basement underlying the Dunsinane deposit.

FERRUGINISED DEPOSITS

Outcrops of ferruginised deposits generally do not exceed 15m in diameter. The ferruginisation is apparently related to localised groundwater activity. This type of deposit occurs throughout the Riversleigh area, particularly along geological boundaries. Around Dunsinane Site such deposits occur in the Precambrian quartzite, overlying Tertiary limestone, and at a point at the junction of the Precambrian quartzite and the Dunsinane sediment, apparently post-dating all of these sediments. In general they consist of pisolitic iron oxide, and iron oxide- enriched alterations of the sediments in which they occur.

OVERLYING TERTIARY LIMESTONES

The hard, micritic, Tertiary limestones directly overlie the Dunsinane limestone. These limestones exhibit vertical changes in colour and frequency of molluscs and calcareous mud clasts, all of which may be construed as primary bedding features. Occasional vertebrate bone fragments occur with molluscs which are very common and well-preserved. Contact of the Tertiary Limestone with the underlying Dunsinane sediment is

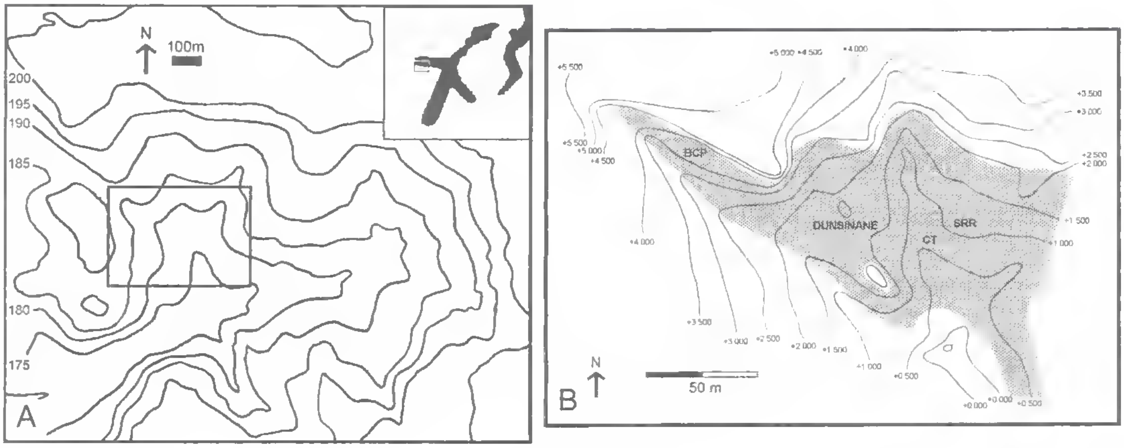


FIG. 1. A, Southern Gag Plateau and Dunsinane Site Local area map. Study area in B outlined. Contours at mAHD. (Southern Gag Plateau map inset from Megirian 1992). B, Dunsinane Site study area indicating the positions of Dunsinane, Bernie's Cooking Pot (BCP), Custard Tart (CT) and Sue's Rocky Road (SRR) Sites. Stipling=Dunsinane limestone. Contours metres from arbitrary field datum.

apparently undulatory, and may be unconformable.

DUNSINANE LIMESTONE

The Dunsinane limestone outcrop is at least 150 m across. It includes the fossil sites Bernie's Cooking Pot (BCP), Custard Tart (CT) and Sue's Rocky Road (SRR) (Fig. 1B), which have previously been regarded as separate sites.

The limestone has been severely weathered, resulting in replacement of most of the original sediment and its sedimentary structures by soft calcrete. Relict unweathered outcrops occur as sandy limestone with apparent flat bedding and minute bone fragments. Because the overlying limestone is closely associated with these relict outcrops, it appears that the weathering event post-dates the deposition and erosion of the overlying sediment.

Because the fine, well-sorted particles and apparent flat-bedding does not indicate high energy flow, the Dunsinane sediment was probably deposited in a pond or lake. This relatively arenaceous sediment was probably deposited under near shore conditions in a quartz-rich Precambrian terrain.

Fossil bones and nodules are preserved with brown iron oxide-rich flourapatite (fluorapatite=calcium fluoride phosphate; $Ca_5(PO_4)_3F$). Energy dispersive X-Ray spectrometry demonstrated that iron oxide appears to be included within euhedral flourapatite crystals. Flourapatite has replaced the majority of structures within nodule matrices. Bones are impregnated with iron-oxide rich flourapatite, particularly around the inner parts. Bones and nodules occur in relict in situ sediment and in the surface layers across the area of the outcrop. Nodule fragments and fragments of fossil wood derived from weathered nodules are common. There are also amorphous concretions of flourapatite and sparry calcite deep within the calcrete (1m depth) in some places.

MODEL OF POST-DEPOSITIONAL HISTORY

Weathering is a striking feature of the Dunsinane sediment. The calcrete is most likely autochthonous because of the relationship between relict unweathered outcrops of Dunsinane sediment and overlying rock. Local groundwater activity has resulted in ferruginisation in the vicinity, although this has not occurred at Dunsinane Site itself. Meteoric and surface water are the most likely agents responsible for chemical weathering of the original Dunsinane sediment.

Severity of weathering has been influenced by permeability of the original Dunsinane sediment, impermeability of the Precambrian quartzite and Tertiary limestone, the situation of Dunsinane Site at the junction of 3 drainage channels, and its position near the top of the local drainage network.

Water focussed on Dunsinane Site by the local drainage system was channelled into the permeable Dunsinane sediment before draining away into the lower catchment. This caused the chemical weathering of the limestone responsible for: 1, apparent subsidence, slumping and surface lowering of the sediment; 2, accumulation of a surface lag of fossils mineralised with insoluble flourapatite; 3, partial dissolution and precipitation of flourapatite bodies deep in the original sediment; and 4, a thin calcareous duricrust which has cemented surface debris.

FLORA AND FAUNA

VERTEBRATES. Due to weathering and poor condition of the fossilised bone, identifiable vertebrate fossils from Dunsinane Site are relatively uncommon. However, there is marked diversity implied by the number of groups present. In contrast with many Riversleigh sites, fish and bird remains have not yet been found at Dunsinane Site. The Vertebrates includes:

Class Reptilia
Order Testudines
Family Chelonidae
genus & sp. indet.
Order Crocodilia
Family Crocodylidae
?*Baru* sp.
Class Mammalia
Order Marsupialia
Suborder Diprotodontia
Family Wynyardiidae
?*Namilamadeta* sp.
Family Diprotodontidae
Subfamily Diprotodontinae
?*Bematherium* sp.
Subfamily Zygomaturinae
?***Neohelos*** sp.
Family Macropodidae
Subfamily Balbarinae
***Nambaroo* sp. nov.**
genus & sp. indet.
Subfamily Balungamayinae
?*Wabularoo* sp.
Order Placentalia
Suborder Chiroptera
Family Hipposideridae
?*Brachipposideros* sp.

Neohelos, *Brachipposideros*, large crocodilians and chelonid turtles which are known from Riversleigh sediments of various Oligocene and Miocene ages are thus not useful for more precise biocorrelation. At Riversleigh wynyardiids are known only from System A and B faunas (Archer et al., 1994). Primitive balungamayine and balbarine kangaroos such as ?*Wabularoo* and *Nambaroo* respectively (the latter appears to be conspecific with a very primitive form from System A White Hunter Site (Cooke, 1997)), are known from Riversleigh System A and B faunas. With the exception of Pleistocene *Diprotodon optatum*, diprotodontines are restricted to System A at Riversleigh (Black, 1997). Thus we regard the fauna as most likely a System A fauna.

INVERTEBRATES

Insect fragments are often quite small, usually around 1mm and include a variety of beetle elytra and beetle prothoraces which show similarities to those of curculionids (weevils) and buprestids (jewel beetles). Curculionids have been found in the Upper Site assemblage (Archer et al., 1994), although the long history of this group makes them of little biostratigraphic use. Termite remains may also be present.

A partial gastropod shell has been identified as a probable terrestrial camaenid (W. Ponder pers. comm. 10/95). Camaenids which are known from the Mesozoic occur in System A (Archer et al., 1994) and are likely to occur in Riversleigh sediments of all ages.

FLORA

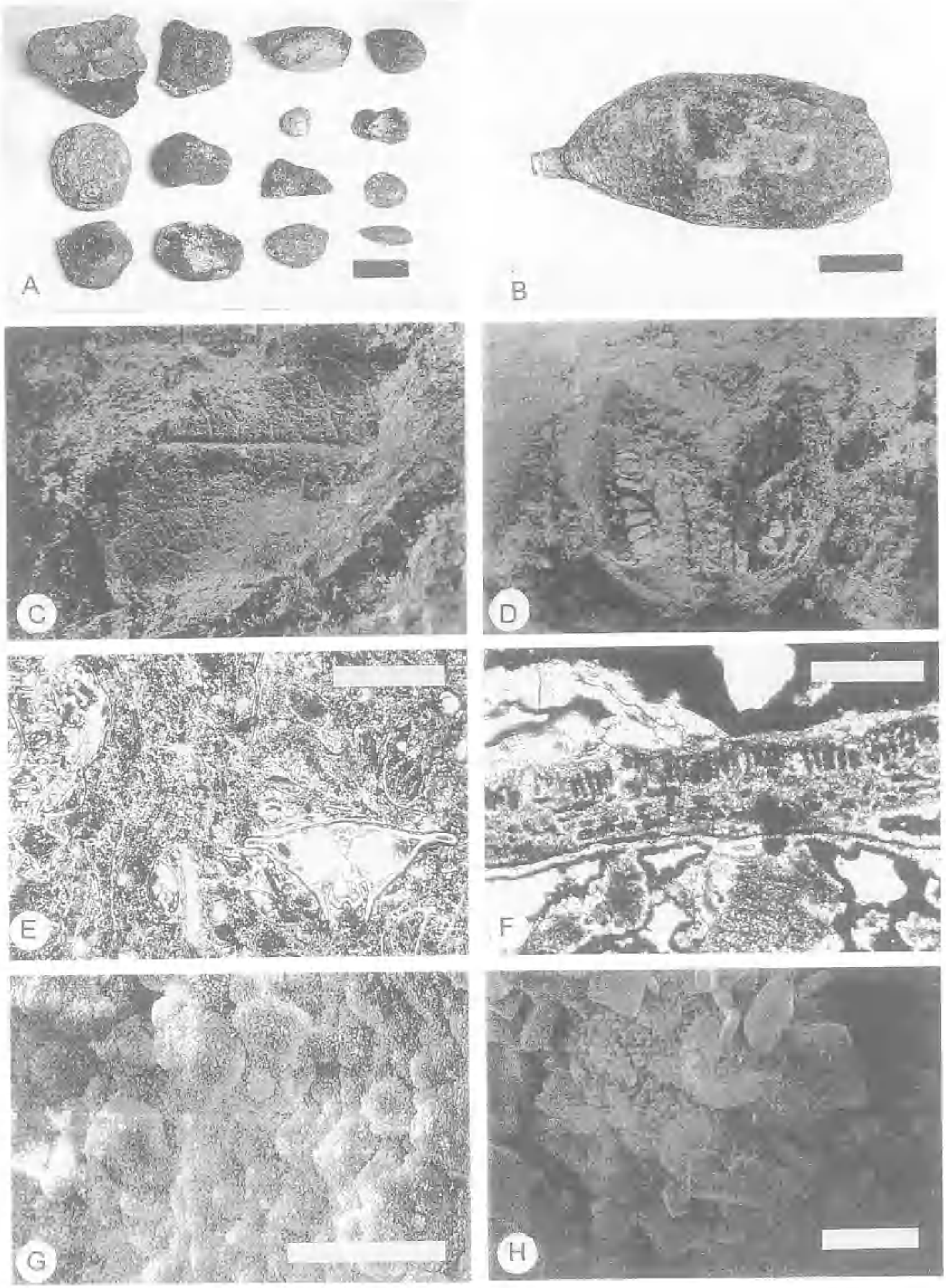
The plant assemblage consists of small pieces of twig-like wood (some stems may originally have been 3-4cm in diameter), leaves, seeds and reproductive organs.

The various types of wood imply high diversity. Angiosperm wood is present as well as probable gymnosperm wood. Leaf fragments are invariably broad and serrate-margined. Leaf cuticles are intact in a number of specimens.

There are several pneumatophore-like organs up to 2cm in diameter with a central aerenchyma of elongate cells and a narrow epidermal layer with structures resembling lenticels.

Groups recognised include Proteaceae, Casuarinaceae, Myrtaceae and possibly Epacridaceae (R. Hill pers. comm. 9/95, 10/96). Proteaceae are evergreen trees and shrubs, and are known from the Early Cretaceous to Holocene (Hill, 1994). The generally xeromorphic Casuarinaceae have a record from the Paleocene to Holocene (Hill, 1994). Myrtaceae are known from the mid-Paleocene to Holocene (Martin, 1994). The Epacridaceae which are prominent in extant scleromorphic floras have existed in Australia since the Late Cretaceous (Jordan & Hill, 1996).

Serrate leaves are not good indicators of a tropical closed forest origin (R. Hill pers. comm.


A
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9/95). Apparent growth rings and false growth rings are evident in some wood samples. Some rings are broad, inferring a long growth season which seems to be terminated abruptly (R. Hill pers. comm. 10/95). In general the associated floristics and the timing of fossil occurrences of epacrids throughout the Tertiary coincide with temperate climatic conditions, and the nature of the macrofossil record is inconsistent with modern tropical or sub-tropical rainforest (Jordan & Hill, 1996). Pollen has been recovered from the nodules but not yet analysed.

PALAEOENVIRONMENTAL IMPLICATIONS

Biocorrelation of the Dunsinane Site fauna with that of White Hunter Site (via *Nambaroo* and *?Bematherium*) allows tentative age assessment. White Hunter Site has been correlated with Etadunna Faunal Zone D (Ngama LF, Lake Palankarinna) on the ilariid, *Kuterintja ngama* (Myers & Archer, 1997). Sediments associated with this South Australian fauna have been palaeomagnetically dated at 24.7-25 Ma (Late Oligocene; Woodburne et al., 1994). This interval coincides with an 'icehouse' event, climatic conditions normally characterised by cooler, drier, seasonal climatic conditions (Frakes et al., 1987). The 'greenhouse'/ 'icehouse' climatic fluctuations of the Tertiary are reflected in the sedimentary and terrestrial fossil records of Australia (Frakes et al., 1987; Archer et al., 1995). The characteristics of the Dunsinane Site flora so far observed may indicate 'icehouse' conditions.

TAPHONOMY

PHOSPHATISATION OF FOSSIL ASSEMBLAGE

Early diagenetic phosphatisation, usually associated with microbial activity, has been identified as the mode of preservation of phosphatic nodules and exceptionally preserved fossils (i.e. Balson, 1980; Müller, 1985; Pinna, 1985; Seilacher et al., 1985; Soudry & Lewy, 1988; Allison, 1988a, b, c; Martill, 1988, 1989, 1990; Lucas & Prévôt, 1991; Briggs & Kear, 1993; Briggs et al., 1993). As confirmed by laboratory experiments (i.e. Prévôt & Lucas, 1986; Hirschler et al., 1990; Briggs et al., 1993; Briggs & Kear, 1993), microbially mediated phosphatisation can occur within or adjacent to bacteria, and can result in the formation of globular apatite microstructures that faithfully preserve the structure of organisms, sometimes at the microscopic level. Conditions under which flourapatite replacement of organic tissue and carbonates may occur are (Lucas & Prévôt, 1991): 1) a concentration of organic phosphorous is required in the system (i.e. the sediment); 2) anoxic conditions which support bacteria capable of precipitating apatite; 3) acidic conditions that destabilise carbonates; these circumstances commonly occur in the interstitia of phosphate-rich sediments. These conditions may be enhanced by 'closure' by a thin film of sediment or bacterial slime, or enclosing structures of organisms or sediment (i.e. carapaces, pore spaces) that contain the optimal environment for apatite precipitation (Krajewski, 1984; Seilacher et al., 1985; Martill, 1988, 1989,1990; Soudry & Lewy, 1988; Hirschler et al., 1990; Lucas & Prévôt, 1991; Wilby & Martill 1992; Briggs et al., 1993; Briggs & Kear, 1993).

Characteristic flourapatite microstructures very similar to those found in fossils from elsewhere in the world thought to be preserved in this way occur in nodule material examined by SEM (Fig. 2 G,H). The lack of distortion or crushing of tissues, preservation of the cellular structures of leaves (see below) and presence of organic material in the Dunsinane nodules indicate early diagenetic, pre-compaction mineralisation. This process is suggested as the mode of preservation for the 3D arthropod fossils from Upper Site (Duncan & Briggs, 1996). Fragments of algal layers in nodule material may indicate thin microbial films that 'sealed' tissues, enclosing conditions favourable to preservation and encouraging and accelerating mineralisation. The Dunsinane nodule material may have mineralised in a water

FIG. 2. A, Dunsinane Site nodules illustrating the variety of shapes and sizes. Scale bar=5cm. B, Some nodules have protusions (in this case a piece of fossil wood). Scale=20mm. C, Leaf fragment. D, QMF31306, a 3-dimensional fruit tentatively assigned to the Epacridaceae. E, Thin section of nodule, entirely phosphatised organic material. Note the undistorted arthropod with cuticle at lower-right. Plane polarised light. Scale=800μm. F, Transverse section of a leaf lamina. The vertically elongated cells are palisade cells, beneath them is intact spongy mesophyll tissue. Plane polarised light. Scale=200μm. G, SEM of nodule material showing the characteristic microstructure of early diagenetically precipitated flourapatite replacing organic tissue. Scale=20μm. H, Globose flourapatite microstructures. The pseudo-hexagonal crystals are flourapatite. Scale=5μm.

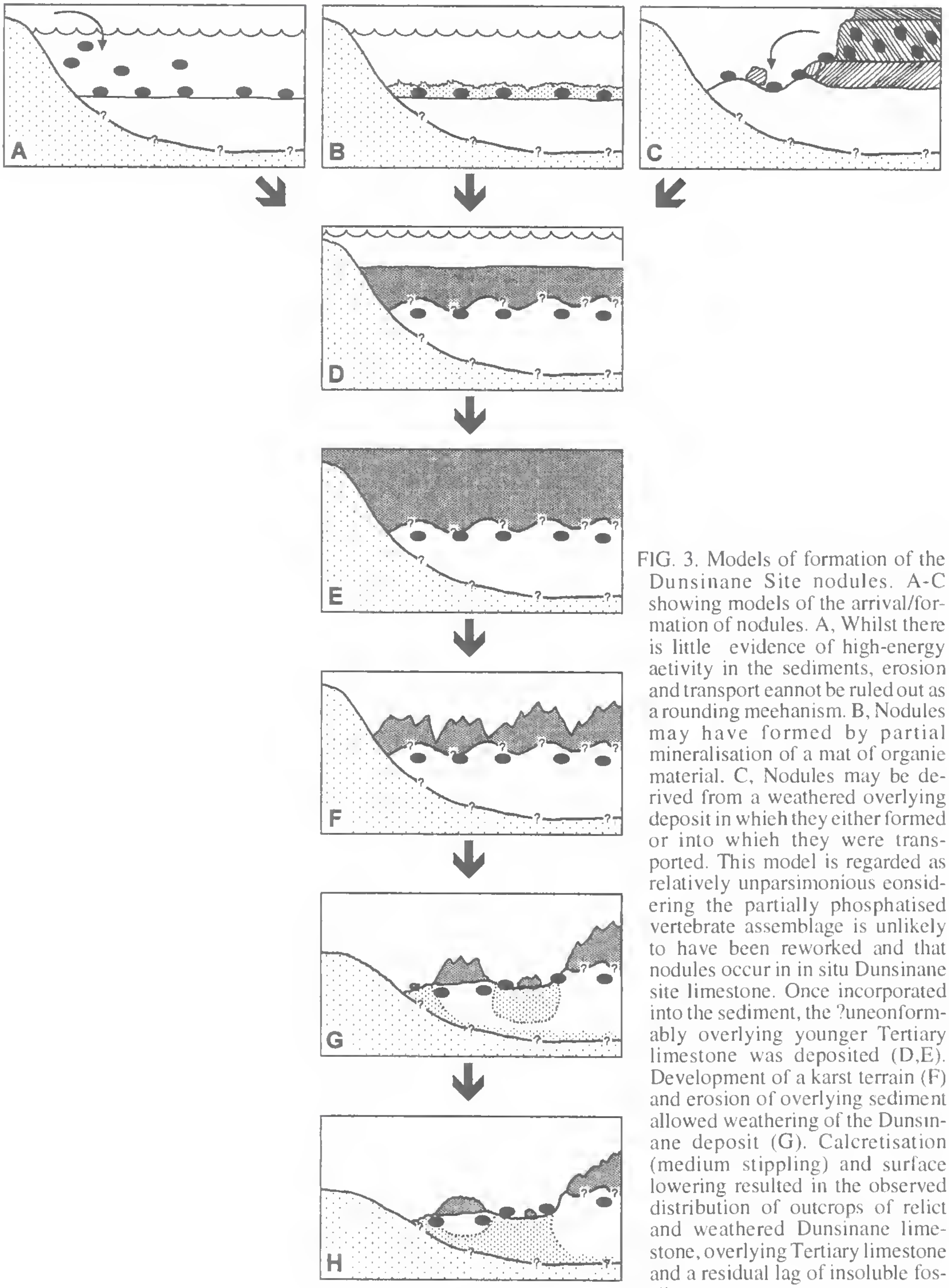

FIG. 3. Models of formation of the Dunsinane Site nodules. A-C showing models of the arrival/formation of nodules. A, Whilst there is little evidence of high-energy aetivity in the sediments, erosion and transport eannot be ruled out as a rounding meehanism. B, Nodules may have formed by partial mineralisation of a mat of organie material. C, Nodules may be derived from a weathered overlying deposit in whieh they either formed or into whieh they were transported. This model is regarded as relatively unparsimonious eonsidering the partially phosphatised vertebrate assemblage is unlikely to have been reworked and that nodules occur in in situ Dunsinane site limestone. Once incorporated into the sediment, the ?uneonformably overlying younger Tertiary limestone was deposited (D,E). Development of a karst terrain (F) and erosion of overlying sediment allowed weathering of the Dunsinane deposit (G). Calcretisation (medium stippling) and surface lowering resulted in the observed distribution of outcrops of relict and weathered Dunsinane limestone, overlying Tertiary limestone and a residual lag of insoluble fossils.

body that had stagnated possibly because of a lack of freshwater input; a proximal acidic anoxic sediment such as peat or influxes of nutrients causing microbial blooms that used up available oxygen and increased available organic phosphorous. As partially decaying organic matter accumulated on and in the substrate, reducing conditions would develop leading to accumulation of iron hydroxides and destabilisation of carbonates (Allison, 1988b) and a proliferation of anaerobic microbes. Phosphatisation may have occurred in tissues in the substrate and close to it, until halted by exhaustion of available phosphate supplies, or dilution of the phosphate-rich medium perhaps by an influx of freshwater supplying oxygen and dissolved calcium carbonate.

PLANT ASSEMBLAGE

Plant organ assemblages composed of twigs, leaves and reproductive organs such as those at Dunsinane Site (Fig. 2C,D) are generally regarded as accumulations with limited lateral wind transport (Collinson, 1983; Spicer, 1980, 1989). Plant assemblages accumulated at the site of growth usually contain roots, wood fragments and plant bases; catastrophic accumulations are poorly sorted and contain components of all types (Collinson, 1983; Spicer, 1989).

Leaves most likely to be preserved in excellent condition are those that fall directly into water, since contact with the ground usually drastically reduces the chances of leaf preservation in an aquatic environment (Ferguson, 1985; Spicer, 1989, 1991). Dissolution of anti-fungal, anti-microbial and structural compounds within leaves begins immediately after immersion or contact with the ground, increasing susceptibility to microbial attack and structural collapse within 24 hours (Ferguson, 1985; Spicer, 1989, 1991). Leaf litter is generally dispersed within 50m of the parent vegetation (Ferguson, 1985; Spicer, 1989, 1991). Hill & Gibson (1986) found that the majority of leaves collected from a lake bed were from species occurring within 50m of the shore. Leaves in the Dunsinane assemblage with limited immersion damage, such as the exceptionally preserved leaf with intact cellular detail (Fig. 2F), may have been derived from vegetation that occurred within 50m of the site of preservation. Since most leaves take hours or days to sink (Ferguson, 1985; Hill & Gibson, 1986; Spicer, 1980, 1989, 1991), buoyant organs such as twigs and seeds are prevalent in the assemblage and are often in quite good condition showing little abrasion or decomposition, and the insect material is so plentiful and diverse these factors may point to the accumulation being in shallow nearshore water.

The plant material thus appears to be part of a proximal assemblage, possibly occurring as an immersed mat of vegetation. The process of mineralisation that preserved the plant material must have occurred in the early stages of degradation since leaves have limited structural damage and intact cellular structure, in particularly spongy mesophyll tissue which is generally the most susceptible to breakdown (Spicer, 1989). The pneumatophore-like organs in the nodule assemblage could indicate anoxic conditions close to the site of preservation.

PROVENANCE AND FORMATION OF THE PHOSPHATISED NODULES

The Dunsinane Site nodules (Fig. 2A,B) may have formed in a variety of ways. Their sub-rounded shape is possibly caused by transport but this is not supported by the lack of any other evidence of high-energy flow. More lightweight fresh clods of organic material may have been sub-rounded by transport and subsequently deposited and phosphatised. However, it is debatable whether the nodule material had been subject to a sufficient compression and consolidation, given the freshness and lack of distortion of some fossil structures. The nodules may have formed at Dunsinane Site, as parts of a mat of fresh organic material resting on the sediment surface. The radiation of mineralisation from points within the mat may have produced the somewhat rounded, but otherwise variably sized and shaped nodules. Roundness of nodules may also be attributed to weathering whilst embedded in the sediment and after exposure, resulting in continuous exfoliation of outer layers.

MODELS FOR ACCUMULATION AND PROVENANCE AND FORMATION OF NODULES (Fig. 3). Allochthony of the nodules must be considered because of their peculiar mineralogy. Intraformational nodules may have formed in an overlying sediment which was weathered, resulting in the descent of sub-rounded nodules to the surface of the Dunsinane sediment and burial by younger Tertiary lacustrine sediment (hence the unconforming contact). However, this is highly unlikely considering that nodules and other flourapatite concretions occur within in situ Dunsinane sediment.

The shared mineralogy of the nodules and vertebrate fossils is compelling when considering contemporaneity. The phosphatisation process can tend to target only those tissues which have a high organic phosphorous content (Balson, 1980; Allison, 1988 a,c), suggesting that Dunsinane Site bones, which show varying degrees of phosphate enrichment, may have been subject to this process when they were fresh and still retained some organic content. This is suggested by the greater enrichment of the inner parts of bone which would have contained high concentrations of organic material. The extreme damage to the Dunsinane Site bone, but lack of evidence of reworking or trampling (particularly in the case of a partially phosphatised, extremely damaged *?Bematherium* skull with dentaries articulated) may indicate damage by the highly acidic conditions in which the plant material was preserved. This would have softened and dissolved bone in the nearby substrate. Nevertheless, the evidence is ambiguous and at this stage.

CONCLUSIONS

Dunsinane Site contains a probable System A vertebrate fauna which may be tentatively dated at 24.7-25 Ma. The fossils from Dunsinane Site are preserved with iron oxide-rich flourapatite, which appears to have precipitated as the result of early diagenetic microbially mediated phosphatisation. The Dunsinane sediment probably formed in a low-energy environment, and has been severely weathered, resulting in a lag of insoluble fossil material on the surface. Relationships of the flora and invertebrate fauna to the other components of the site are as yet unresolved.

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